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Species Diversity at Wet Tropical Environments II. Speciation of *Schismatoglottis okadae* (Araceae), an Adaptation to the Rheophytic Habitat of Mountain Stream in Sumatra

Hiroshi OKADA and Mitsuru HOTTA

ABSTRACT *Schismatoglottis okadae*, a rheophytic species, was investigated on its distribution pattern, habitat, morphology, karyotype and population structure.

The species is restricted to a few locations in West Sumatra which are separated from each other. In these places (locations) the species occurs only in the area near the stream. The stem and leaf show mat-rooted characteristic which is typical to other rheophytes.

The chromosome number is $2n = 26 + 0 \sim 8B$. But, one structural mutation of chromosome is present and it can be applied for the analysis of colony structure just as the presence or absence of B-chromosomes. As the results, two kinds of colony structure have been detected: one is composed of homogeneous individuals, which seems to have propagated vegetatively, and the other is heterogeneous which would have developed from seedlings.

The speciation of the group in the Barisan range is presumed to occur through the following processes: the geographical upheaval of the Barisan range provided the new ecological niche, rapid streams, for the rheophytic forms. The ancestral form of this species might have existed near the mild stream of the mountain plateau as to be seen in Airsirah plot site today, from which true rheophytic forms adapted to the rapid stream sides have been produced.

KEY WORDS: Araceae/ B-chromosome/ cytotaxonomy/ population structure/ rheophyte/ *Schismatoglottis okadae*/ speciation/ tropics

Introduction

So many papers and essays have been published regarding the richness of tropical flora and the speciation in the tropical rain forests (Ashton, 1969; Cain, 1969; Corner 1967; Dobzhansky 1950; Fedorov, 1966, 1976; Richards, 1969; van Steenis 1957, 1969, 1976), but we still lack adequate information to realize fully the mechanisms of their speciation processes in such tropical environments. The speciation mechanism of rheophyte is not clarified yet (Kato, 1983). This study may further provide the answer for the question what kinds of phenomena occurred at the early stages of development of the rheophytic form and for the question how the speciation is now proceeding under such peculiar environments.

The occurrence of the rheophytic form along rapid streams in Malesia is one of the interesting phenomena in terms of evolutionary trends of plants in the tropical rain forests. This type of speciation, viz. adaptation to specialized habitat, has been already discussed in details by van Steenis (1981) on its occurrences in many unrelated groups of plants. According to him, the thick coriaceous and lanceolate leaves, developed strong root system, creeping rhizome etc. are characteristic features common to these mat-rooted rheophytes growing on rocky place beside rapid streams. The

present paper may answer to some extent for the question postulated by Kato (1983) what phenomena occur on the speciation at these rheophytes.

In the first paper of this series, we have described and discussed the polymorphic variations and population structure of *Schismatoglottis lancifolia*, a forest floor herb of tropical rain forests (Hotta et al. 1985). *S. okadae* M. Hotta of Sumatra is very close to *S. lancifolia* by its spathe and spadix characters, but it exhibits a striking contrast to the cited species in the habitat, morphological and reproductive characters and in the population structure to which our research is primarily directed. In this study we document the distribution, ecology, cytological and morphological diversity, and population structure of *S. okadae*, and discuss the speciation process of *S. okadae* as a species fitted to the rapid stream sides.

I. Materials and Locations

Four locations (31 sites) as indicated in Table 1 were chosen to analyze the population structure of *Schismatoglottis okadae*. The details of these locations are as follows:

Karang Putih (KP) is situated on the western slope of the Barisan range, while Airsirah is on the eastern slope of the same range. The latter is composed of two locations: one is around Airsirah forest plot (AP) and the other is in near Kampung (villege) Airsirah (KA). Bukit (hill) Gadang (BG) lies on the eastern slope of the Barisan range, but it is far remote from Airsirah and located on the area of the different river system.

Karang Putih location (KP) is situated at low elevation, about 250–300 m alt., and the river passes a sandstone zone (upper area) and a limestone zone (lower area) (Fig. 2–A). The location is densely covered with primary riparian forest. The river is about 10–20 meters wide forming a steep gorge, and the stream side is rather open and bright. Compact and dense colonies of *S. okadae* grow along this bright stream side. The river runs toward the western direction and pours into the Indian Ocean at Padang city.

Airsirah location (AP) is situated at ca. 1100 m alt. and a rather flat place covered with a montane oak forest, near to Airsirah forest plot (Fig. 2–B). Sites of this location form loose colonies. Colonies spread linearly over about 30 m in distance along small streams.

Kampung Airsirah location (KA) is situated ca. 800 m alt. and located at downstream of the same river system of the former location (AP) (Fig. 2–C). Collection sites are all located on a sunny gentle slope, and forests beside the stream were already cut down for agricultural purposes. AP and KA locations are separated from KP location by the main ridge, the watershed of the Barisan mountains, and the stream flows to the opposite direction to that of KP pouring into the Malacca strait through Sungai (river) Induragiri.

Bt. Gadang location (BG) is ca. 800 m alt. and isolated from three other locations about 60 km to the south (Fig. 1 & 2–D). This location is well covered with the riparian forest except around the water falls there. Compact and dense

Table 1. Location, site (colony), sampling individual number, stem decumbency and ecological notes of *Schismatoglottis okadae* of West Sumatra

Location	Site (Colony)	I. No.	Stem decumbency In Field	In Cult.	Ecological notes
	A	3	+	+	Small** linear colony at shaded wet limestone rock beside stream
	B	7	+	+	On pebble bed near site A, large** colony
	C	3	+	+	Same as site B, small colony
Karang Putih	D	9	+	+	Wet pebbley place near stream, open place, colony forming large patch
(KP)	E	6	+	+	Near site D, open place, medium** colony
Alt. ca.	F	4	+	+	Shaded sandy place near stream, small colony
400 m	G	8	+	+	Shaded sandy place near stream, large colony
	H	4	+	+	Shaded sandy place near stream, small colony
	I	5	+	+	On shaded wet rock, small colony
	J	9	(+)	−	Pebbly wet place near small water-fall, large compact colony (2×2 m)
	K	18	+	+	On shaded wet rock around small water-fall, large colony
	L	10	+	+	Sandy wet place beside stream, large colony
	M	7	+	+	Pebbly wet bed beside stream, linear medium colony at semiopen place
	N	3	+	+	Small colony near site M, shaded
	O	2	+	+	Same as colony N
	P	5	+	+	On wet rock near stream, linear medium colony
	Q	9	+	+	On wet rock near stream, large colony
Kampung Airsirah	A	5	+	+	Clayey wet river bank, open place
(KA)	B	11	+	+	Clayey wet river bank about 20 m downstream of site A, open place, large colony
Alt. ca. 800 m	C	14	+	+	On wet rock near stream, semishaded, large colony
Near Airsirah Plot	A	3	(+)	−	On wet stream side clayey bank, shaded, loose small colony
(AP)	B	3	(+)	−	About 5 m downstream from site A
Alt. ca. 1100 m	C	10	(+)	−	On wet rock beside stream, about 10 m downstream from site B, shaded, medium colony
	D	5	(+)	−	On wet rock beside stream, about 10 m downstream from site C, shaded, large colony
	E	6	(+)	−	Close to site D, semiopen place
Bukit Gadang	A	4	+	+	On wet rock near water-fall, well shaded, large colony
(BG)	B	2	+	+	Pebbly bed beside stream, large colony, semishaded
Alt. ca.	C	5	+	+(−)*	On wet rock near water-fall, large colony
800 m	D	2	+	+	Sandy bed beside stream, large colony
	E	2	+	+	On wet rock beside stream, small colony
	F	3	+	−	On wet rock near water-fall, large colony

I. No.=Sampling individual number.
* One of five individuals possessed slightly erected stem in cultivated condition.
** Colony size: Large=colony occupied wider area than 2 m². Medium=colony occupied about 1 m². Small=colony occupied narrower area than 0.5 m².

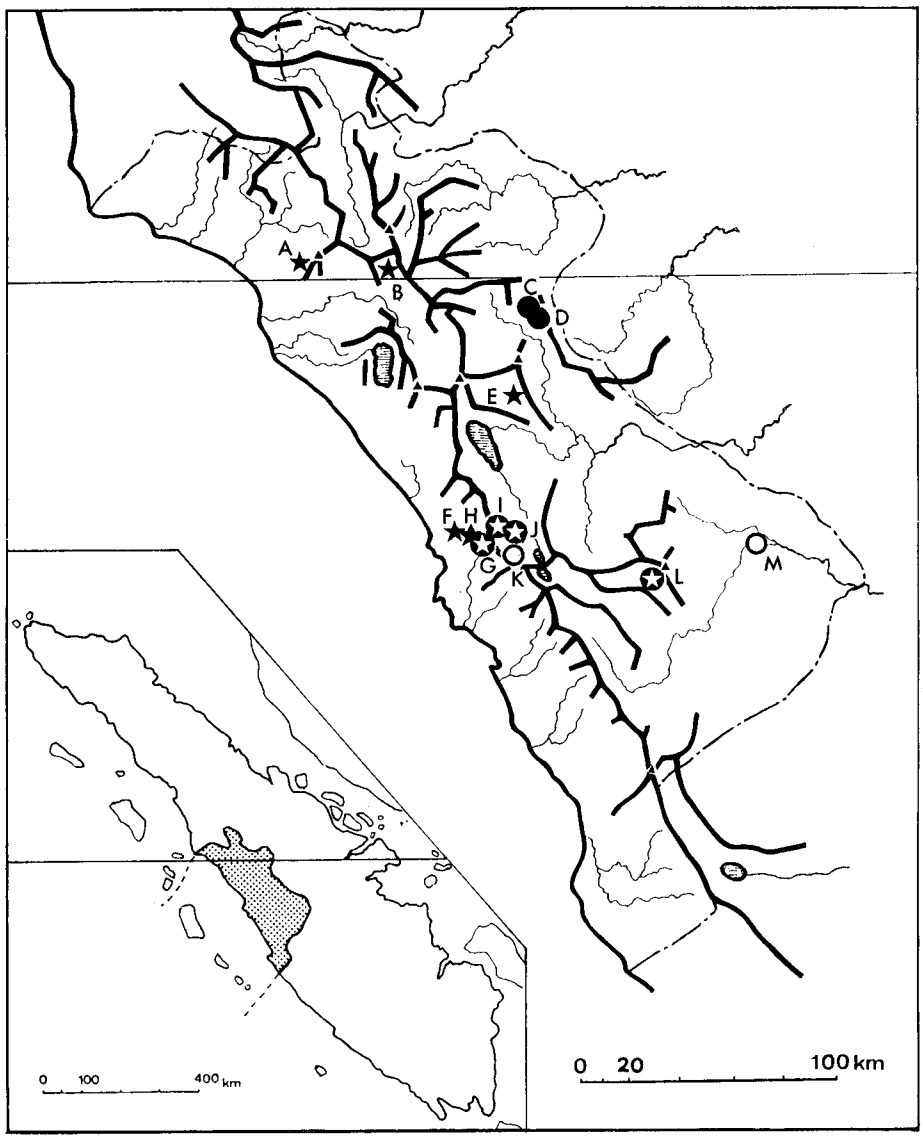

Fig. 1. The map of study sites at West Sumatra showing main ridges of Barian range, river systems and locations.
A. West side of G. Talamau. B. Lurah Berangin. C. Harau. D. Kelok Sembirang. E. Batusangkar. F. Limau Manis. G. Karang Putih. H. Ulu Gadut. I.Near Airsirah plot. J. Kpg. Airsirah. K. G. Talang. L. Bt. Gadang. M. Sg. Daleh.
★ *Furtadoa sumatrensis* ● *Homalomena rusdii* ✪ *Schismatoglottis okadae* ○ *Others*

colonies of *S. okadae* occur together with rheophytic *Impatiens* sp. The stream goes down to Malacca strait through Batang (river) Hari which belongs to the different river system from that of AP and KA locations.

Fresh materials were collected randomly from some colonies in AP, KA and KP in January and August of 1981, in September of 1984, and those from BG in Sep-

tember of 1985 (Table 1). In all those cases the apical parts of stems were cut off 3–5 cm long and planted in the experimental garden of the Department of Biology, Andalas University and then brought to the green house of the Kyoto University and Osaka University, Japan, for morphological and cytological observations. A few duplicate clones are cultivated in the Bogor Boranical Garden.

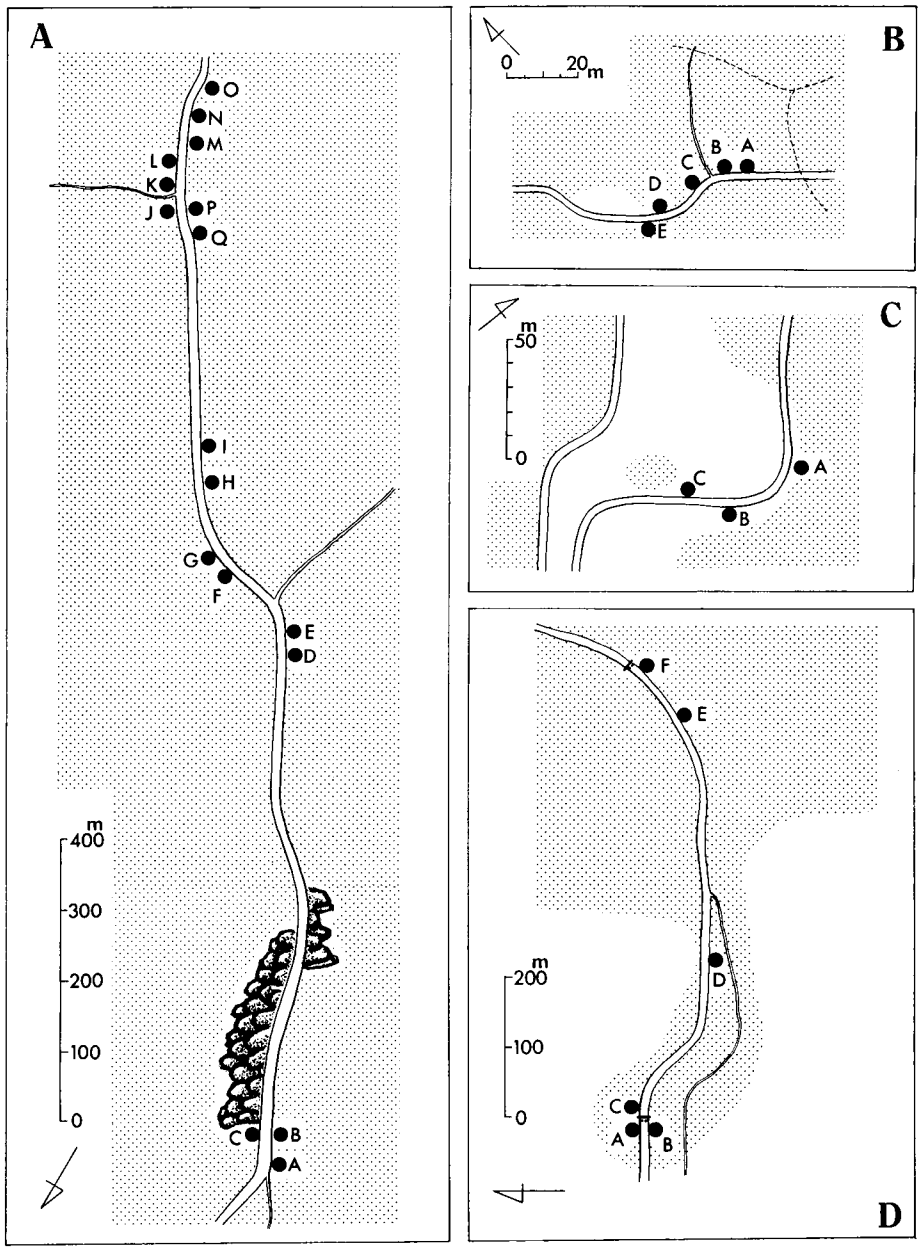

Fig. 2. Sketch maps of collecting sites of each location. Dotted areas are covered with forest. A. Karang Putih. B. Near Airsirah plot. C. Kpg. Aitsirah. D. Bt. Gadang.

II. Habitat and Allopatric Distribution of Allied Rheophytes

The habitat of *Schismatoglottis okadae* is always established beside streams (Fig. 3). The light intensity of the habitat is quite different between sites (see Table 1, ecological notes). Some sites are extremely bright (KA–A & B; KP–A, B, C, D & L; BG–C, D, E & F), while some other sites are dark under the close forest canopy (AP–A, B, C & D; KP–F, G, H, I, J, K & N; BG–A & B). The species grows on various beds, such as a wet rock of various origin (limestone, sandstone and volcanic rocks), pebbly ground, and sandy or clayey soils. Undoubtedly this species has a wide range of adaptability with respect to light and ground condition. Nevertheless, its habitat is limited to narrow flooded zone of the stream and it does never grow beyond the upper level of the flood.

The stems spread entangling together and are fixed strongly by roots on rocks or on the ground. When stream is flooded by heavy rainfall, plants sink under the stream as the other rheophytic plants, but their habitats may become dry when stream level goes down. Therefore, the species must tolerate against two quite different severe conditions: the strong stream flow and the dryness.

In West Sumatra, among the Barisan range there are distributed various kinds of rheophytic aroids (Fig. 1, Table 2). Four of five such species are strictly rheophytic, viz. *Schismatoglottis okadae*, *Homalomena rusdii*, *Furtadoa sumatrensis* and *Scindapsus* sp., while one another, *Schismatcglottis batoensis* is a facultative rheophyte. Through our extensive research of the area the distribution of these species has been clarified (Hotta, ed. 1984, 1986 and Table 2). Accordingly *Furtadoa sumatrensis* is distributed to the northern

Fig. 3. A large population of *Schismatoglottis okadae* around small water-fall, Bt. Gadang, alt. ca. 800 m.

Table 2. The distribution of rheophytic species studied at West Sumatra

Location	Rheophytic species (Araceae) S.O*	(S.B)*	F.S*	H.R*	SCI*	(Others) PHY*	IMP*	OSM*	DIP*
Lurah Berangin	−	−	+	−	−	−	−	−	−
Gn. Taramau (west side)	−	−	+	−	−	−	−	−	−
Harau	−	−	−	+	−	+	−	−	+
Kelok Sembilan	−	−	−	+	−	−	−	+	−
Batusangkar	−	−	+	−	+	−	−	−	−
Limau Manis	−	−	+	−	−	−	−	−	−
Ulu Gadut	−	+	+	−	−	−	−	−	−
Karang Putih	+	−	−	−	−	−	−	−	−
Near Airsirah plot	+	−	−	−	+	−	−	−	−
Kpg. Airsirah	+	−	−	−	−	−	−	+	−
Gn. Talang (west side)	−	+	−	−	−	−	+	−	−
Bt. Gadang	+	−	−	−	−	−	+	−	−
Sg. Daleh	−	−	−	−	+	−	−	−	−

* S.O: *Schismatoglottis okadae.* S.B: *Schismatoglottis batoensis* (occasionally occurs in stream side, facultative rheophyte). F.S: *Furtadoa sumatrensis* H.R.: *Homalomena rusdii.* SCI: *Scindapsus* sp. PHY: *Phyllanthus* sp. IMP: *Impatiens* sp. OSM: *Osmunda vachellii.* DIP: *Dipteris lobbiana.*

part of West Sumatra, while *Schismatoglottis okadae* is endemic to the southern part of the region. *Homalomena rusdii* occurs only at the restricted area around Harau Nature Reserve in Payakumbuh, eastern part of the region. In the Ulu Gadut Valley, east of Padang city, there are two rheophytic aroids; *Furtadoa sumatrensis* and *Schismatoglottis batoensis*, but they are clearly separated and segregated their habitat, such as the former species is only at Sg. Lantik, the branch of the Ulu Gadut Valley, while the later species occurs at Sg. Gadut Gadang, Sg. Gadut Ketil and Sg. Lumui, i.e. the central and southern branch of the same valley. In each location mentioned above the rheophytic habitat is occupied by only single species of rheophytic aroids with exception of *Scindapsus* sp., which may grow by mixture with the other species in some cases. Such an allopatric distribution of the rheophytic aroids has been observed in Borneo (Hotta, per. ob.), and it is also typically present in Sumatra. The exceptional cases are very rare.

III. Morphological and Reproductive Characteristics

Unlike the other allied species of the genus, *Schismatoglottis okadae* commonly shows the rheophytic characteristics of stem and leaf.

Rheophytic Habit

All of the individuals of this species show the decumbent and branched stem in the fields (Table 1). In the cultivated condition, however, all of the individuals from the location AP, one colony from the locations KP (KP–J) and one of BG (BG–F)

Fig. 4. Stem decumbency in cultivated condition.
Left: Decumbent stem with positive geotropism (BG-C).
Right: Erect stem with negative geotropism (BG-F).

show erect stems through negative geotropism (Fig. 4).

A leaf of this species is characterized by a deep green subcoriaceous lamina which shows lanceolate, narrower cordate or cordate shape and cuneate to rotundate or cordate base in the field (Fig. 5). This feature seems to well adapt to the stream flow. The leaf index (I: ratio of length to width, van Steenis 1981) of this species is usually around or larger than 2.0 ($I \geqq 2.0$), but individuals of the location AP and of KP–J indicate lower value, i.e. less than 1.8, and have cordate lamina. The leaf index of rheophyte usually shows $I \geqq 4.0$, with some exceptions of the lower value, $I = 2 \sim 3$ (van Steenis, 1981). The

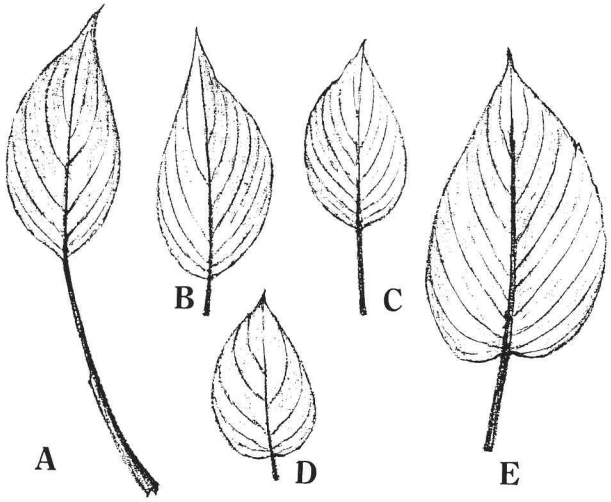

Fig. 5. Leaf shape of *Schismatoglottis okadae* from different locations. The laminae show wide variations; from broad to narrow in shape and from cordate to cuneate at base. ×2/5. A. KP-H-2. B. KP-M-4. C. KP-F-1. D. KP-J. E. AP-B.

leaf shape of this species is preserved in cultivated condition, but usually it becomes slightly wider. The leaf index value of this species indicate that this species does not adapt to strong stream flow yet. Despite of its subcoriaceous leaf texture and long fibrous petiole, this species seems to well adapt to the stream side.

Vegetative Reproduction

Individuals in a colony propagate mainly by vegetative reproduction, or in a few cases, by seeds. New stems branch out at nodes frequently, while old ones become decayed. Some of individuals which are apparently independent plants undoubtedly originated from one seedling. They form a patch like colony with several net work-like stems spreading a few meters square. In fields it is impossible to identify their individuality based on the genetical homogeneity. As the stem elongates 1–2 cm per month in cultivated condition, therefore, it is presumed that the medium size colony (1×1 m) may have been established in 5 years even in favorable condition.

Rapid stream flow occasionally cuts off stems. These stems can grow up to mature plants at a new place judging from our experience of easy cultivation from the stem cuttings. Thus, the species may expand the distribution area along the stream not only by seeds but also by cutting stems. Even where colonies are isolated from one another by different plant communities or by physical barrier such as stream, rocks, etc., there is a possibility that some of them are descendent from the same individual.

The vegetative propagation is considered to be very important and effective system for quick dispersal and exact establishment of colony of the rheophytic species *S. okadae* in the same river system towards the downstream sites.

Fruit Dispersal

The species has another propagation system, the dispersal by small fruits (seeds) as in *S. lancifolia* (Hotta et al. 1985). In the case of the latter species, its small fruits were usually carried by ants and renewed quickly the population by seedlings (Hotta et al., 1985). However, in the case of *S. okadae* small seeds and seedlings may be easily carried away by stream flood which occurs frequently.

The distribution of *S. okadae* is, at present, extremely restricted. Indeed, the species occurs only at a few locations in southern part of West Sumatra (Fig. 1), namely, around Airsirah, Karang Putih and Bt. Gadang. This long distance distribution can not be explained by the stream dispersal alone. We assume some other effective dispersal mechanisms across the mountain ridge or to the different river system. It must be the fruit (seed) dispersal. The carrier of the fruit is not certainly identified, but herbivorous land tortoises, which we have frequently met within G. Gadut area, or the small mammals or torrent birds may be the agents of for the long distance carriers across the ridge of the mountain.

IV. Chromosome Variation

The chromosome number of root tip cells of *S. okadae* is counted as $2n=26$ with

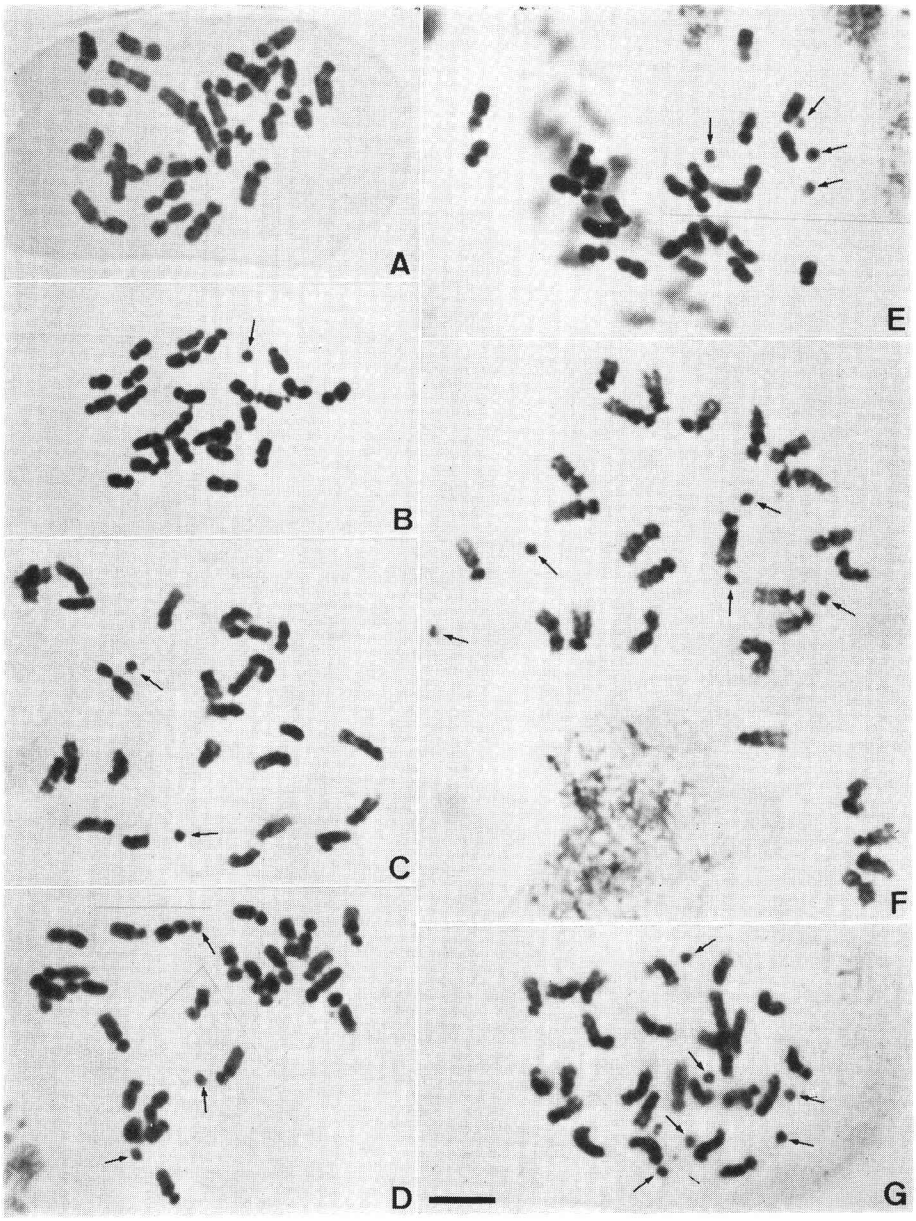

Fig. 6. Photomicrographs of somatic chromosomes of *Schismatoglottis okadae*. 2n=26+0~6B. A; mutant of chromosome structure. 0B-chromosome. B—G; 1B~6B. Bar, 5 μm.

0 to 8 small extra chromosomes in all of the individuals observed* (Fig. 6).

The chromosome complement of this species consists of almost similar chromo-

* Chromosome observations on somatic cell division were made following the same methods as those described elsewhere (Hotta et al., 1985). Presence or absence of B-chromosome was judged on the basis of more or less 10 cells.

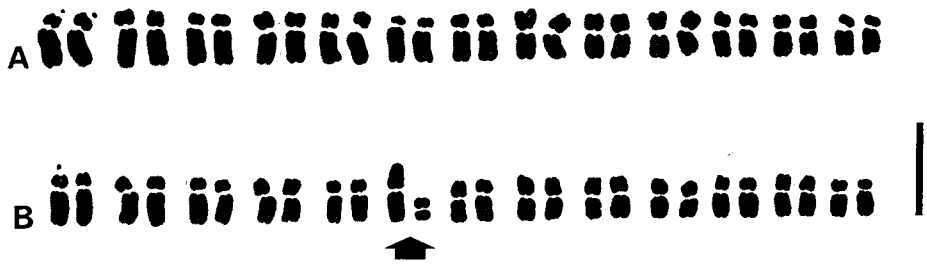

Fig. 7. Somatic chromosomes at metaphase of *Schismatoglottis okadae*. 2n=26. A; the common chromosome complement. B; the mutant of chromosome structure (arrow). Bar, 5 μm.

somes to that of *S. lancifolia* (Fig. 7A, cf. Hotta et al., 1985). Chromosome length ranges from about 3.0 μm to 2.0 μm gradually. There are 3 pairs of metacentric chromosome and 10 pairs of acrocentric one. The first pair are an acrocentric chromosome with a satellite of about 0.3 μm in length at the distal end of the short arm. They seem to correspond to "J" type satellite chromosome of *S. lancifolia*.

The structural mutation of chromosome is found in all of the individuals of no. J colony at Karang Putih. The 11th and 12th chromosomes form a heterogeneous pair as shown by arrow in Fig. 7B. The 11th chromosome is the largest metacentric chromosome of about 3.3 μm in length, while the 12th chromosome is the smallest metacentric one of about 1.3 μm in length. Both chromosomes are easily distinguishable from the others in size and shape. It is presumable that they originated from two similar (homologous) acrocentric chromosomes like as the 11th and 12th chromosomes of the other individuals (Fig. 7A). A total length of the 11th and 12th chromosomes of both chromosome complements represented by Fig. 7A and B is almost similar to each other. The reciprocal translocation might have occurred on both chromosomes at the near region of primary constrictions. These kinds of chromosomes are not found in the other individuals. Although many mutations at satellite chromosome were found in *S. lancifolia*, *S. okadae* did not show any other mutations.

In addition to autosome complement, there are small extra chromosomes of about 1 μm in length, known as B-chromosomes, in some individuals as in *S. lancifolia* (Hotta et al., 1985). Marchant (1971) has also reported similar extra chromosome in *S. concinna* var. *immaculata*.

A numerical variation of B-chromosome is found among cells of the same individuals (Fig. 8) as in the case of *S. lancifolia* (Hotta et al., 1985). B-chromosomes of *S. okadae* are probably identical to those of allied species as mentioned in a previous paper. The similar numerical variation of B-chromosome in somatic cells was reported in many other unrelated species, for example, *Allium cernuum* (Grun, 1959), *Aster scaber* (Matsuda 1970), *Claytonia virginica* (Lewis et al., 1971), *Xanthisma texanum* (Semple, 1972, 1974), *Silene maritima* (Cobon & Murray, 1983), and etc. Grun (1959) observed that in *Allium cernuum* the number of metacentric B-chromosome is more stable than that of telocentric ones. Matsuda (1970) reported different distribution patterns of B-chromosomes between root tips in the same clone of *Aster scaber*. Type

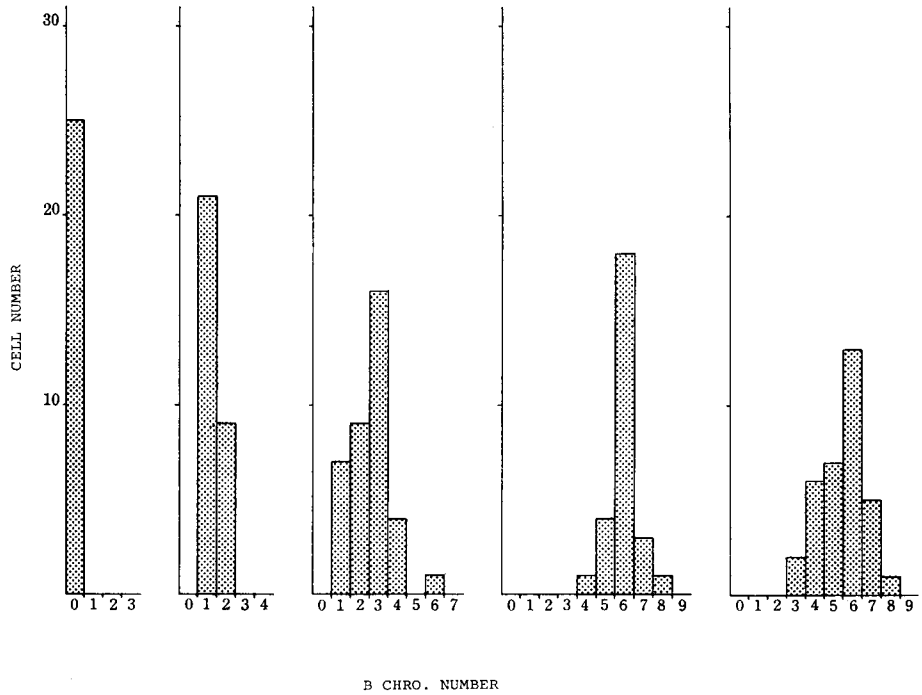

Fig. 8. Diagrams showing the numerical variation of B-chromosome in the different individuals. The individual without B-chromosome shows constancy of the B-chromosome character.

iso_p B-chromosome shows the constancy in number between cells in the same clone, while number of type a_s varies between cells as the result of a nondisjunction at somatic cell division.

The observations of 25 to 37 root tip cells in five individuals of the present species indicate that the numerical variation takes a wide range in case of individuals with many B-chromosomes, but shows the constancy in case of individuals with 1 or 0B (Fig. 8). The individual of KP–G–4 at Karang Putih location varies B-chromosome number between cells ranging from 3 to 8 with the mode at 6, while all cells of individual KP–J–7 lack B-chromosome. Individuals at Airsirah location, which are presumed to have propagated vegetatively, consistently have only 1B in any cell. Peculiar behavior of B-chromosome of this species might be caused from two kinds of B-chromosome as in the cases of *Allium cernuum* and *Aster scaber*. The difference between 0B and 1B seems to be very stable. Therefore, the character in terms of presence or absence of B-chromosome seems useful for population analysis.

V. Population Structure

The results of character analysis mentioned above show the aspect that there are two kinds of internal structure of colonies. The one consists of homogeneous individuals; the other comprises heterogeneous ones. The colony KP–J of Karang

Table 3. The variations of B-distribution and stem decumbency under cultivated condition at colonies of each location of *S. okadae*. The difference of numbers between Table 1 and 3 is caused by death in cultivation. Bold letters: the complex colonies. *: mutant at 11th and 12th chromosome.

Location		KP	KA	AP	BG
colony no.		A B C D E **F G H** I J K L M N O	**A B C**	A B C D	A B C D E F
No. ind. + or − B-chro.	+	0 0 1 0 2 2 3 1 0 0 0 0 1 2 0	0 5 2	1 1 5 1	0 0 0 0 0 0
	−	1 3 0 1 0 1 1 1 2 8 *4 1 0 0 2	2 2 1	0 0 0 0	4 2 5 2 2 3
stem decumbency	+	1 3 1 1 2 3 4 2 2 8 4 1 1 2 2	2 7 3	0 0 0 0	4 2 4 2 2 0
	−	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	0 0 0	1 1 5 1	0 0 1 ? 0 0 3

Putih, for example, is constructed by homogeneous individuals (Table 3). All of 8 individuals examined possess the distinctive heterogeneous chromosome pair, i.e., the 11th and 12th chromosomes, but do not have B-chromosomes (Fig. 7B). In general, progenitors with heterogeneous chromosome sets do not generate the homogeneous offsprings. If individuals grew up from seedlings, this colony had to contain various combinations of these chromosomal mutations. The uniformity of chromosome complements among 8 individuals indicates that colony KP–J is constructed by only one clone which propagated vegetatively. The same aspect appeared in colonies KP–B and K and KA–A where only individuals with no B-chromosome grow, and the colony AP–C where only individuals with one B-chromosome are distributed. All of the colonies at location BG also show the uniformity with respect to the cytological character of individuals.

On the contrary, some colonies (Table 3) are constructed by different seedlings judged from the complexity of B-chromosome distribution. For example, the colony KA–B consists of, at least, two clones; individuals with B chromosomes vs. those without B-chromosomes. Exact detection of clone number in these colonies is not accessible. The colonies KP–F, G and H and KA–C also contain individuals of different origin.

Thus, the colonies of this species are classified into two categories: one is established from single seedling, and the other from plural ones. The latter may contain the snapped or broken stems which were swept down from upper stream.

Colonies of the same location are distributed linearly along the stream. The distance between two colonies is sometimes less than 10 meters. The locations KP and KA show the similar aspect concerning the morphology of constituent of B-chromosomes, that is, both locations consist of both heterogeneous and homogeneous colonies in terms of the B-chromosomes (Table 4). Furthermore, the latter colonies are composed of B-chromosome containing and B-chromosome lacking colonies. Each colony of the location BG shows homogeneity on cytological character. All individuals from this population have no B-chromosomes. In the field, individuals of this population bloomed and set good fruits. The leaf character (Leaf Index) slightly varied between colonies. Furthermore, this location contains both clones of positive and negative geotropism in cultivated condition. These evidences suggest the heterogeneity

Table 4. Colony and clone number observed karyotype in each location. Colony number is excluded in case of single observation.

location	colony homo/hetero		B containing clone + / −	
KP (Karang Putih	7	3	7	11
KA (Kpg. Airsirah)	1	2	2	3
AP (Airsirah)	4	0	4	0
BG (Bt. Gadang)	6	0	0	6

of this population. Therefore, it is concluded that these three locations are constructed by individuals which are generated by both seeds and vegetative system.

On the contrary, the population AP consists only of homogeneous colonies. It clearly appears in B-chromosome distribution and the negative geotropism of stem. It is possible to say that this location is established from a single seedling. If individuals were dispersed by seeds, they should show the heterogeneity with respect to B-chromosome. B-chromosomes randomly behave in meiosis, so that various kinds of gamete concerning B-chromosome component may occur. B-chromosome of this species is considered to have no genetical activity as in the case of *S. lancifolia*, so that there is no necessity to consider its advantage at the high elevation and/or dark environment. Individuals in cultivated condition have erect stems and cordate leaves. The chromosome homogeneity in this location indicates that the vegetative propagation is a prevailing system. Individuals do not form a dense and patch-like colony, but are rather dispersed. The environment of the dark montane forest may decrease their reproductive activity. Actually we could observe neither flowers nor fruits in this location, though transplanted individuals in a green house well bloom. The vegetative propagation by accidental stem snap may be the only effective propagation and dispersal system at this location.

In general, the rheophytic plants receive strong stream pressure when rain falls heavily, and a part of their stems are occasionally carried off from their growing places. This condition causes the increase of the opportunities to the vegetative propagation of *S. okadae*.

VI. Discussion and Conclusion

Dispersal and Isolation

The distribution areas of *S. okadae* are classified into three groups from viewpoint of river systems; 1) Karang Putih (KP), 2) around Airsirah (AP, KP), and 3) Bt. Gadang (BG).

The population BG is clearly different from the others in respect of no B-chromosome distribution. B-chromosome is common karyological characteristics in *Schismatoglottis lancifolia-okadae* group. The location BG is situated 60 km far from two other locations. We have not discovered any locations of this species at any places around Gn. Talang, the active volcano. This volcano is located between Bt. Gadang

and the other locations. Either the founder effect (or the bottle neck effect) or effective geographical isolation may result the difference in the component of B-chromosomes from the other locations. It may be said that the seed carriers move out narrow range, and a few immigrants invaded this area. This population is undoubtedly established by limited genetic sources which have no B-chromosome.

The watershed of Barisan range lies between locations KP and KA. This species is restricted to the habitat at the places beside stream. Therefore, the isolation efficiency for each location is extremely distinctive. The distribution range of *S. okadae* linearly spreads along stream by the scattered fruits and by the decumbent stems. Both are carried downstream. In any case the expansion of distribution against the stream or into the places far from streams seems unlikely to occur. Nevertheless, these two locations, KP and KA, have many common characteristics in morphological and karyological features. Frequent immigrant by seeds may also occur.

We compared two populations, AP and KA, within the same river system on the basis of the morphological characters. The individuals of location AP are not completely specialized into rheophytic forms yet. They have, for example, cordate leaves and erect stems in cultivated condition (in field, stems are decumbent). All individuals within this location appear to propagate vegetatively as mentioned above. The location KA is positioned at the downstream of AP location. It is reasonable to consider that populations at the downstream contain individuals from the upstream. There are, however, no individuals in the population KA which have the common characteristics of those of the population AP. In spite of belonging to the same river system, these two populations have no close connection. Strong selection pressure may have effected the survival of individuals with disadvantageous characters at rapid streams.

Speciation at Unoccupied Ecological Niche

In West Sumatra there are some places where many rheophytic individuals grow. No cases are, however, observed in which allied taxa grow sympatrically (Table 2). It is a general phenomenon that only limited rheophytic species grow at narrow space beside stream. Very rare cases are observed at Borneo region in which more than two allied taxa grow at the same area and are mixed up there. Although the genus *Schismatoglottis* diverges into many species at Malesia region, there are very few rheophytic species: for example, *S. homalomenoidea* group and *S. monoplacenta* group at Borneo. In Borneo island the habitat beside rapid streams is usually occupied by the other allied genera, namely, *Piptospatha, Aridarum, Bucephalandra, Heteroaridarum* and *Hottarum*. These are endemic or subendemic genera to Borneo and are considered to have diverged from a common ancestral stock of *Schismatoglottis* (Hotta 1982). The specialization to rheophytic forms in *Schiamatoglottis* and *Homalomena* might be inhibited by these endemic genera which already occupy the ecological niche. On the contrary, the rheophytic species of *Homalomena* and its allied *Furtadoa*, e.g., *H. consobrina* group, *H. elliptica, H. nutans, H. rusdii, F. sumatrensis* and etc., abundantly occur at Malay Peninsula and Sumatra island. Endemic genera of Borneo island men-

tioned above are absent at these regions. From the viewpoint of ecological niche, the lack of rheophytic genera allied to *Schismatoglottis* at Sumatra was favourable or even necessary for the speciation of *S. okadae*.

Speciation Process

Based on comparison of the different appearances of the geotropism within this species, as well as on consideration of the relationships between this specialized species and its allied species which show the negative geotropism (erect stem), it is suggested that the species diversed originally at the upper or gentle stream side of mountain region. All individuals at the location AP show uniform characters of the erect stem under the cultivated condition. The genetic control of geotropism is not strictly fixed yet at the location AP.

We propose an idea for speciation process of a new rheophytic species, *S. okadae*, as follows:

1) A certain ancestral form of *S. okadae*, which probably resembles *S. lancifolia*, spreads out at montane area of Barisan range. The area contained various contrasting environments, such as, gentle vs. steep slope, slow vs. rapid stream, gorge vs. ridge, and etc.

2) The ancestral form of *S. okadae* invaded a side of slow stream. There were no rheophytic aroid taxa of Sumatra origin, nor Bornean rheophytic taxa. An ecological niche that was not occupied by any taxa was thus available for newly evolved species.

3) This ancestral form rapidly developed rheophytic features, such as decumbent stem and coriaceous narrow leaf lamina. In this way only individuals with those advantageous structures could establish new habitats at a side of rapid stream.

4) At a side of slow stream, it might not yet elapse enough period to develop and fix genetically the rheophytic structures, or selection pressure might not be effective for individuals with unstable genetic systems.

Historical Effect for Speciation

There are many rheophytic taxa diverged at Borneo island. Many rheophytic aroid species and genera are known in this region (van Steenis 1981). With respect to the species level, however, there are also many species of rheophytic aroids diverged from the ancestral form in Sumatra, where we have efforts of survey. They are seemingly of recent origin. This indicates that the environment of Sumatra region has the capacity to induce the rheophytic form as a pioneer. Among them, we have two distinct rheophytic aroid species, *Furtadoa sumatrensis* M. Hotta (1981) and *Homalomena rusdii* M. Hotta (1985). In the original description (Hotta, 1981) *Furtadoa* was reported as the endemic genus to Sumatra, but the other species, *F. mixta* (Ridl.) M. Hotta, is recently found at Malaya Peninsula. *Homalomena rusdii* is a peculiar species among the genus in having the basal placentation and the free ligule of petiole base. This species, however, is closely related to *H. consobrina* (=*H. paucinervia*). Both species has the basal placentation and the narrow coriaceous leaf lamina. There is no reason to remove *H. rusdii* into a new separate genus from *Homalomena*. On the basis

of the analysis of rheophytic aroid flora, we safely conclude that the rheophytic flora of Sumatra island diverged less frequently than that of Borneo. The reason why no endemic genera have developed in Sumatra is to be considered that these rheophytic species have recently diverged at the geologically young Barisan range. It may have not yet elapsed enough period for establishing an endemic genus in Sumatra as in Borneo region. *Schismatoglottis okadae* is the species that has just been established as a rheophyte in the Barisan range.

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